Histology of ganoid scales from the early Late Cretaceous of the Kem Kem beds, SE Morocco: systematic and evolutionary implications

by

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Abstract. – In 1963, N. Tabaste described disconnected fossil material from the Saharan Cenomanian site of Gara Tabroumit, and especially three sets of isolated scales that she all referred to the genus *Lepidotes*. Although the rhomboid shape and overall morphology of one set of scales allow regarding them as ganoid scales, the external aspect of the ganoine is not as regularly smooth and shiny as it is in most lepidosteoid scales commonly referred to ginglymodian ("semionotiform") fishes. A photonic microscopic study of scale ground sections definitively excludes the allocation of these scales to the genus *Lepidotes*, or to closely related genera, because of an interrupted ganoine layer, and, more generally to ginglymodians: *i*) the bony basal plate is deprived of Williamson's canaliculi, which characterized holostean scales; *ii*) the basal plate is well vascularised and overlaid by a thick layer of dentine; *iii*) there is an elasmodine layer between dentine and the basal plate. These various histomorphologic characters allow us to consider these ridged scales as belonging to a polypteriform fish, probably *Bawitius*. The histological specificities of the two other scale series allow their allocation to holostean taxa, respectively to "*Lepidotes*"*pankowskii* and to *Obaichthys africanus*. A new generic name, *Adrianaichthys*, is coined for *"Lepidotes" pankowskii*.

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Résumé. – Histologie des écailles ganoïdes du site des Kem Kem, SE du Maroc (base du Crétacé supérieur) : implications systématiques et évolutives.

En 1963, N. Tabaste a décrit, dans le site Cénomanien Saharien de Gara Tabroumit, du matériel fossile déconnecté, et tout particulièrement trois séries d'écailles isolées qu'elle a toutes attribuées au genre *Lepidotes*. Toutefois, nous avons été intrigués par l'aspect de la ganoïne à la surface de certaines écailles. Effectivement, si leur forme rhomboïde et leur épaisseur, associées à un faible recouvrement, permet de les ranger parmi les écailles ganoïdes elles n'ont pas une surface lisse régulière de ganoïne comme cela est décrit pour les écailles lépidostéoïdes des poissons ginglymodes ("semionotiformes"). L'étude microscopique de ces écailles, fondée sur des lames minces, permet de rejeter définitivement leur attribution au genre *Lepidotes,* et d'une façon plus générale leur appartenance à un ginglymode. Effectivement *i*) la plaque basale osseuse est dépourvue de canalicules de Williamson, structures qui caractérisent les holostéens ; *ii*) elle est abondamment vascularisée et recouverte d'une épaisse couche de dentine ; *iii*) une couche d'élasmodine est localisée entre la dentine et la plaque basale. Ces différentes caractéristiques histomorphologiques permettent de considérer ces écailles à ganoïne irrégulière comme appartenant à un Polypteriforme, probablement du genre *Bawitius*. En revanche, les caractéristiques histologiques des deux autres séries d'écailles sont compatibles avec celles des écailles des holostéens, respectivement "*Lepidotes*" *pankowskii* et *Obaichthys africanus*. Un nouveau nom de genre, *Adrianaichthys,* est donné à "*Lepidotes*" *pankowskii*.

Key words
Polypteriformes
Ginglymodi
Bawitius
Lepidotes
Obaichthys
Adrianaichthys
Morocco
Cenomanian
Gonadoid scales
Paleohistology

Numerous fossiliferous beds yield unconnected elements, which are too incomplete to be referred to specific taxa on the basis of morphological characteristics only. Nevertheless, paleohistological techniques often allow taxonomical attributions at the order or family levels, at least. For example the first Mesozoic African polypterids were characterized owing to paleohistological studies of isolated scales (Gayet *et al*., 1988; Smith *et al*., 2006), as well as the first Mesozoic South American Polypteriformes (Gayet and Meunier, 1991, 1992; Meunier and Gayet, 1996, 1998; Dutra and Malabarba, 2001).

In Africa, several early Late Cretaceous formations are known for their rich fossil ichthyofaunas. The Mesozoic outcrops of the Kem Kem Beds in Morocco have yielded well preserved specimens (Dutheil, 1996, 1999a, b; Cavin and Brito, 2001; Filleul and Dutheil, 2001, 2004; Cavin

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and Forey, 2004, 2008; Forey and Cavin, 2007; Forey *et al.*, 2011), as well as the Bahariya locality in Egypt (Weiler, 1935; Stromer, 1936; Schaal, 1984; Grandstaff *et al.*, 2012) and localities in Niger and northern Sudan (Werner, 1993), among others. In addition, North African localities also delivered a fossil fish record composed of numerous isolated bones, in particular vertebrae, scales and teeth (Weiler, 1935; Stromer, 1936; Casier, 1961; Schaal, 1984; Werner, 1993, Le Loeuff *et al.*, 2010; Benyoucef *et al.*, 2015). The Kem Kem Beds (Morocco) have yielded numerous disconnected material such as teeth, scales and isolated fragments of skull (Khalloufi *et al.*, in press). N. Tabaste (1963) described from the Saharan Cenomanian site of Gara Tabroumit, disconnected fossil material, especially isolated scales. She referred three sets of scales to the genus *Lepidotes*, family Semionotidae, and a fourth set to *Stromerichthys*, the latter being now referred to *Obaichthys* (Grande, 2010).

The external morphology of ganoid scales show homoplasic characters, such as a rhombic shape, a regular ganoine surface, a peg and socket articulation (Schultze, 1977; Janvier, 1996; among others). These characters are shared by different clades, and consequently the taxonomic attribution of isolated ganoid scales can be erroneous when only based on morphological features. However, taxonomic assignment can be improved with morphological specific features, such as the microtubercles at the surface of the ganoine (Gayet and Meunier, 1986; Gayet *et al.*, 1988; Meunier and Gayet, 1996) and/or with accurate histological data (Schultze, 1966, 1968, 1977; Meunier and Brito, 2004). Among the three different scale morphologies referred to "*Lepidotes*" by Tabaste (1963), we were intrigued by one of them, in which the external morphology was incompatible with that of a ginglymodian taxon. Although the rhomboid shape of these scales, their thickness and the thin layer of ganoine allow to attribute them to the ganoid type, their surface is not regularly smooth and shiny as described in the lepidosteoid scales of ginglymodian fishes (Goodrich, 1907; Schultze, 1977; Sire *et al.*, 2009). These peculiar scales show few shiny ridges overlaying a matt surface. We had the opportunity to do a histomorphological study of the material analysed by Tabaste, together with some new isolated material coming from the Kem Kem beds in Morocco. Here, we provide the descriptions of these various isolated scales, which constitute a complement to the recent systematic revision to the bony fish assemblage from the Cenomanian of the Kem Kem beds in Morocco (Cavin *et al.*, 2015).

MATERIAL AND METHODS

Material studied

MNHN-HGN 93, MRS 45, MRS 52. – Material studied by N. Tabaste (1963) and collected by Lavocat from Gara Tabroumit (see Tabaste, 1963). At least 3 to 4 scales from each type.

MNHN-Histos 1959-1989. – Material from the Cenomanian Kem Kem beds, collected by one of us (DD, private collection). Ground sections registered in the National Museum of Natural History of Paris.

Methods

Ground sections. – The scales were embedded in stratyl resin (Chronolite 2060). Transverse and longitudinal sections were performed with a sawing machine; the sections were ground and polished to obtain adequate thickness for a microscopical observation (50-80 μm). They were observed with a microscope "Axiovert" in transmitted natural light and polarized light.

Peel observations. – Replica of the scale surfaces (peels) were done with cellulose acetate films. Peels were examined by phase contrast microscopy and a quantitative study of the dimensions of the microtubercules (when present onto the ganoine surface) was done with "Image J" software (Eustache *et al.*, unpubl. data).

SEM observations. – Scale surfaces were coated with a gold layer (20 nm thick) and examined in secondary electron imaging mode, with the scanning electron microscope "TESCAN VEGAII LSU" operating at 15 kV.

SYSTEMATIC PALAEONTOLOGY

Holostei Müller, 1844 (*sensu* Grande, 2010)
Ginglymodi Cope, 1872 (*sensu* Grande, 2010)
LEPISOSTEIFORMES Hay, 1929 (*sensu* López-Arbarello, 2012)

Adrianaichthys gen. nov.

Type species. – *Adrianaichthys pankowskii* (Forey, López-Arbarello & MacLeod, 2011)

Diagnosis. – As for the type and only known species, see Forey *et al.* (2011).

Etymology. – In honour of Adriana López-Arbarello, palaeoichthyologist at the Bayerische Staatssammlung für Paläontologie und Geologie, München, who undertook the difficult task to untangle the phylogeny and systematics of ginglymodian fish, and '*ichthys'* (fish in Greek).

Remarks. – In their original description of *"Lepidotes" pankowskii*, Forey *et al.* (2011) pointed out the heterogeneous status of the genus "*Lepidotes"*, which was at that time in urgent need of revision. López-Arbarello (2012), in a revision of several ginglymodian taxa, did not include this species in her phylogenetic analysis, but suggested that "*L.*" *pankowskii* is most probably a lepisosteiform incertae genus.

In subsequent articles dealing with this species, the genus *Lepidotes* was generally quoted between inverted comma (Bermúdez-Rochas and Poyato-Ariza, 2015; Benyoucef *et al*., 2015) or preceded by a question mark (Cavin *et al*., 2015). In order to clarify this situation, a new genus name is coined. Among other characters, *Adrianaichthys* gen. nov. differs from *Lepidotes* as defined by López-Arbarello (2012) by its first anterior infraorbital bone not deeper than the more posterior anterior infraorbitals, three pairs of extrascapulars (versus one) and eight suborbitals, four of which lying in front of the orbit. According to López-Arbarello (2012), *Adrianaichthys pankowskii* shows characters of Lepisosteiformes, such as scales with rostro-caudal articulation through anterior dorsal and ventral processes, co-ossified vomers, three or more pairs of extrascapulars, closed circumorbital bone ring, and large supraorbital bone longest ventrally, contacting more than one infraorbital bone. We include here *A. pankowskii* in the Lepisosteiformes, pending a revision of the species.

RESULTS

Morphology

All studied scales have a rhomboidal shape; they are thick with a small cover of enamel (Fig. 1). The whole sample of scales can be divided in four types according to their ornamentation.

Type I. The first series regroups thick and large rhomboid scales with a regular ganoine layer on the surface; the latter looks altered probably because of erosion (Fig. 1A, B). Some scales with a sagittal symmetry had a medio-dorsal localisation on the back of the fish. Some other scales have two anterior processes, which protrude from the anteroventral and anterodorsal corners. These two anterior processes have been observed in the scales of many specimens assigned to "*Lepidotes*" and closely related genera (Cavin *et al*., 2009; López-Arbarello, 2012). Such scales with a regular ganoine cover are common in the Kem Kem beds and were referred to *Adrianaichthys pankowskii* (Cavin *et al*., 2015). However, the worn surface of the ganoine layer of these scales prevented the observation of possible thin microreliefs.

Type II. The scales of this type have a shiny surface with antero-posterior ridges (Figs 1C-E), the median one being frequently more pronounced with a posterior sharp extremity (Fig. 1D). These scales, which were previously referred to *Stromerichthys* (Weiler, 1935; Casier, 1961; Tabaste, 1963; Jonet, 1971; Torices *et al*., 2012; Vullo *et al*., 2009), belong to *Obaichthys africanus* (Grande, 2010; Cavin *et al*., 2015). SEM examinations of the ganoine ridges have revealed microtubercles (not illustrated). Peels studies indicate that these microtubercles are large and closely packed, as in *Lepisosteus* scales (Gayet and Meunier, 1986).

Types III and IV. Two series of scales share an irregular surface of ganoine (Fig. 1F-I). The first series is constituted by 10-20 mm-broad scales showing either irregular patches (Fig. 1F) or more or less parallel and ramified ridges (Fig. 1H) of ganoine. The second series regroups scales that are less than 10 mm in length and bear a ganoine cover made of parallel shiny ridges (Fig. 1G-I). In these two series, the scale surface looks matt between the ridges or the patches of ganoine (Fig. 1F-I). We refer these scales to "paleoniscid" fish, possibly a polypteriform such as *Bawitius*. We do not consider *Bawitius* as a Polypteridae because of the interrupted ganoine layer (see Dicussion).

SEM examinations of the palaeoniscoid scale surface (Fig. 2A) have revealed various, minute ornamentations, but we have not observed microtubercles on the whole surface of ganoine (Fig. 2B, C). They have been either worn out by erosion or, more likely, originally missing, except in the rim of some ganoine patches (Fig. 2D) (see Discussion); here and there the ganoine of the ridged palaeoniscoid scales showed microreliefs, either microtubercles and/or thin elongated hollows (Fig. 2D, E). The scales with irregular ganoine

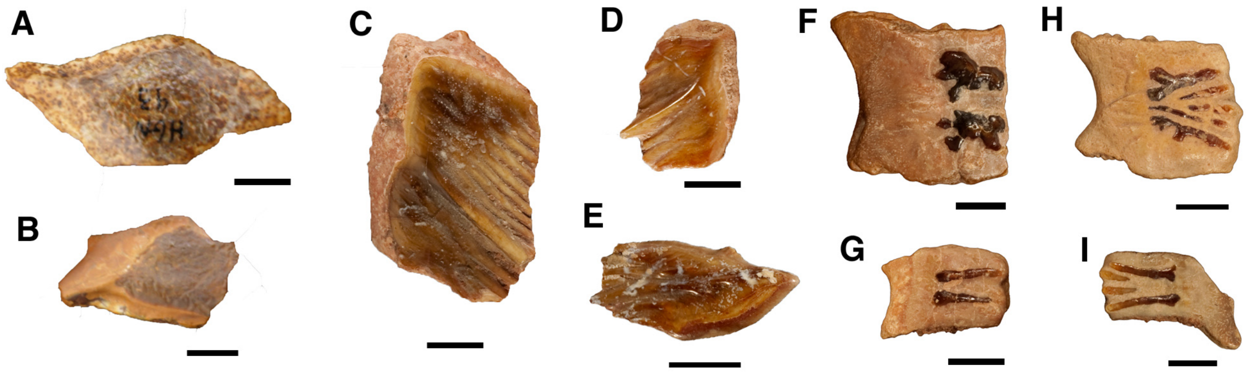

Figure 1. - Isolated scales of the Kem Kem beds. **A, C-H**: Scales studied by Tabaste (1963). **A**: *Adrianaichthys* sp. (fig. 9, Pl X); **B**: *Adrianaichthys* sp., scale sampled by one of us D.D.; **C-E**: *Obaichthys* sp. (figs 6, 7, 9, Pl XI); **F,H**: *Bawitius* sp. (figs 4, 5, Pl XI); **G, I**: Palaeonisciformes (figs 1, 2, Pl XI). Scale bars: A, B, F-I = 1 cm; C-E = 5 mm.

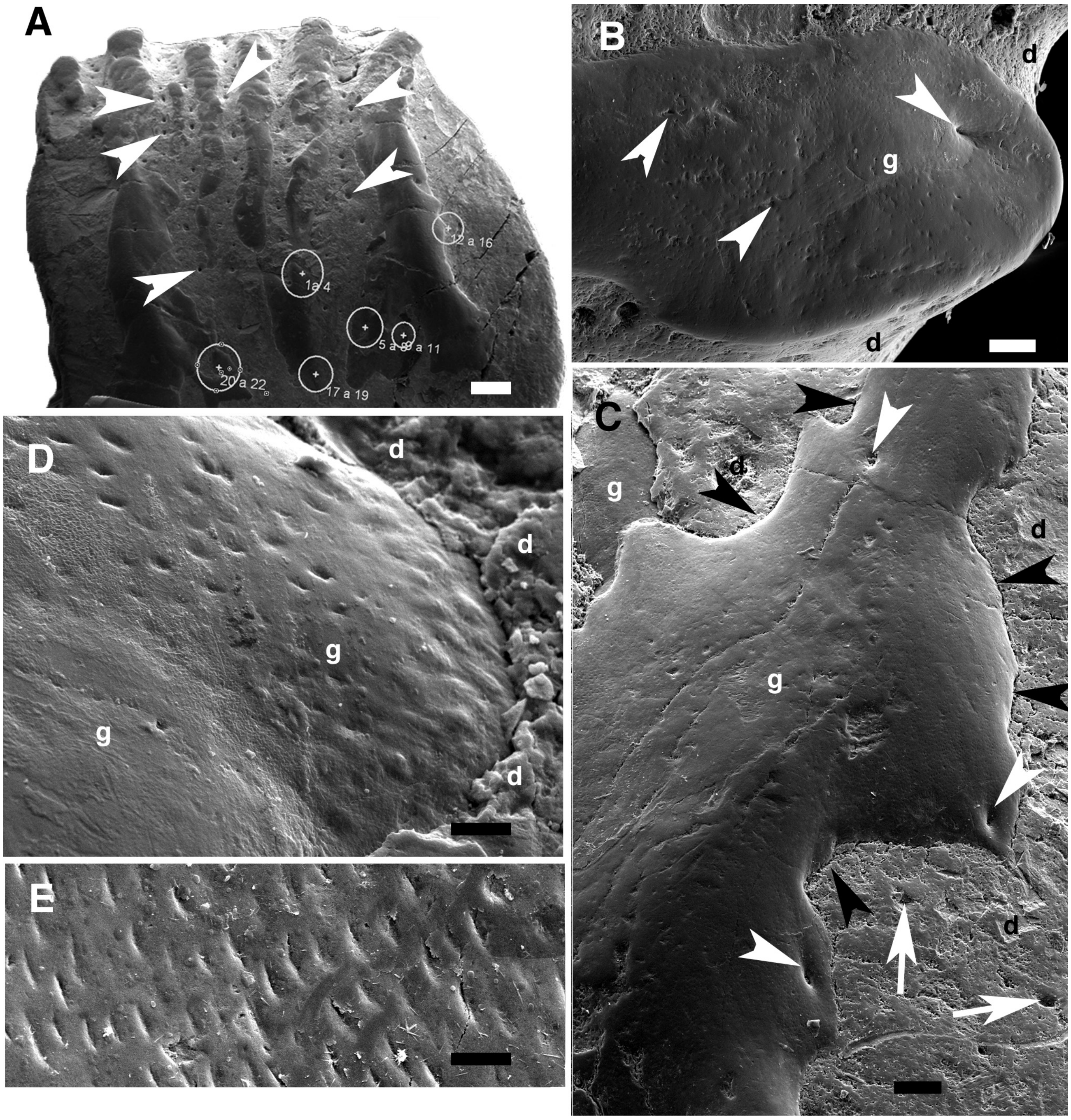

Figure 2. - Scales of *Bawitius* (SEM). Upper surface. **A**: A ridged scale. The circles and the arrowheads localize respectively the areas of the observation of ganoine microreliefs and vascular apertures; **B**: Detail of the posterior extremity of a ganoine ridge. The contact between the ganoine and the dentine looks regular. Vascular apertures on the ganoine surface are visible (arrowheads); **C**: Detail of a ganoine ridge showing its contact with dentine (black arrowheads). The white arrowheads and arrows point to holes indicating vascular canal apertures respectively at the surface of ganoine and at the surface of dentine; **D**: Detail of ganoine near the dentine layer showing some microtubercles on the right and elongate hollows on the left; **E**: Detail of ganoine at the surface of a ridge showing the thin elongate hollows. (**d** = dentine; **g** = ganoine). Scale bars: A = 500 μm; B = 25 μm; C = 100 μm; D, E = 10 μm.

layer show numerous apertures at their surface (Fig. 2B, C) in contrast to types I and II.

Histology

Type I, Adrianaichthys pankowskii *(Fig. 3A-D)*

These scales show only two layers (Fig. 3A): 1) a superficial, pluristratified ganoine layer (Fig. 3B) that covers the whole surface of the scale, except its posterior margin, and 2) a thick basal plate made of pseudolamellar bone (Fig. 3A, B). The bone is cellular and is crossed by numerous ascending canaliculi of Williamson (Fig. 3B, C), 2.5-4.0 μm in diameter; some of them are dichotomized (Fig. 3D). This basal plate is nearly avascular (Fig. 3A), and contains numerous Sharpey's fibres (Fig. 3C) and growth marks (Fig. 3B, C). Dentine has not been observed between the ganoine layer and the bony basal plate.

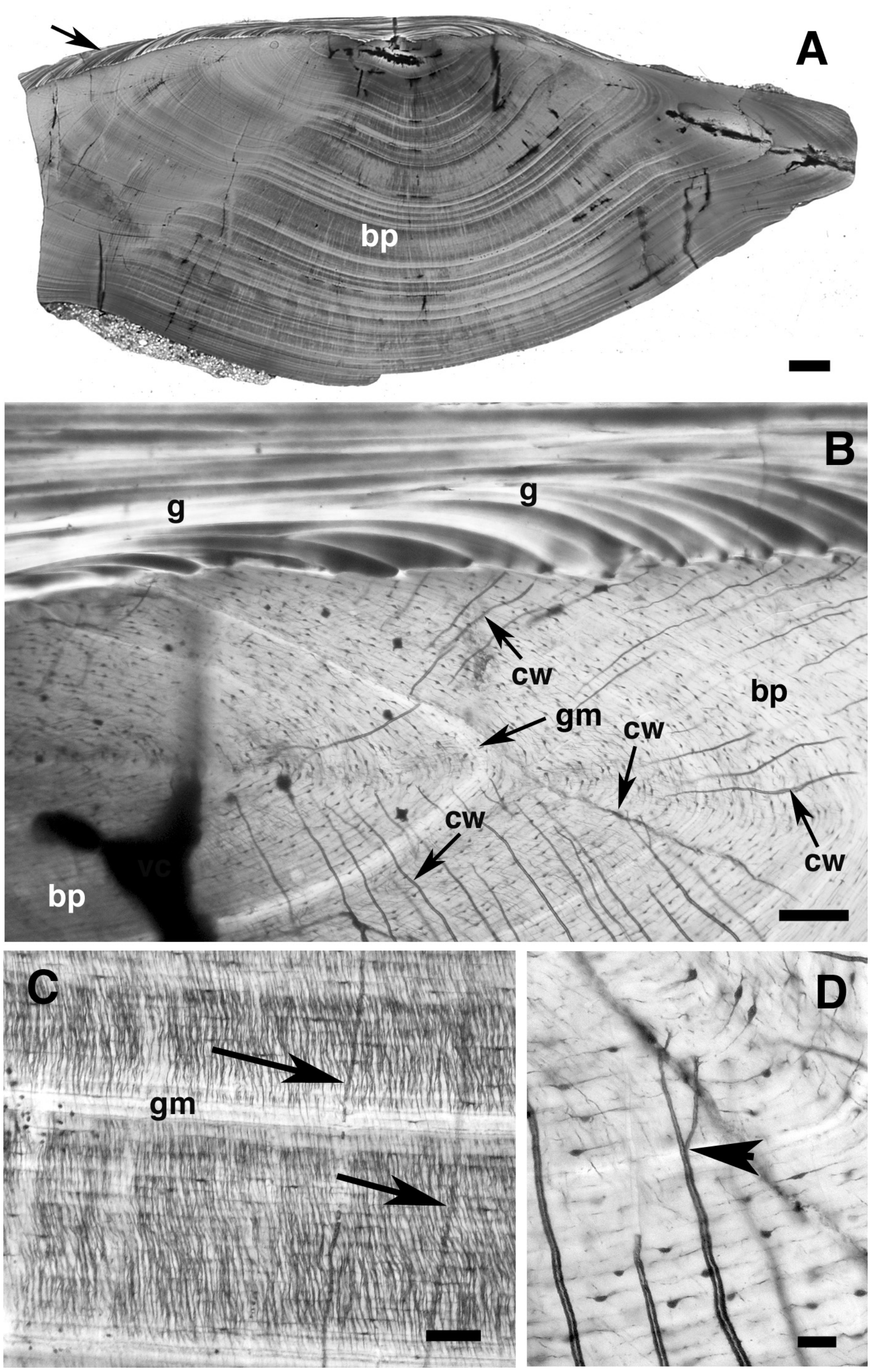

Figure 3. - Scales of *Adrianaichthys pankowski* (MNHN-Histos 1959). **A**: Cross section of a scale (transmitted natural light) showing two superimposed layers: pluristratified ganoine (black arrow), and basal plate (**bp**) constituted of an avascular bony tissue. Dentine is lacking; **B-D**: Cross sections of scales (transmitted natural light); **B**: Detail of pluristratified ganoine (**g**). In the underlying bony basal plate (**bp**) one can see canaliculi of Williamson (**cw**) and a growth mark (**gm**); **C**: Detail of the bony basal plate showing numerous Sharpey's fibres and two canaliculi of Williamson (arrow) and a growth mark (**gm**); **D**: Detail of the bony basal plate showing a dichotomy on a canaliculus of Williamson (arrowhead). Scale bars: A = 1 mm; B = 100 μm; C = 50 μm; D = 20 μm).

Type II, Obaichthys africanus *(Fig. 4A-H).*

The surface of the scales shows antero-posterior ridges (Figs 4A, B), covered by an uninterrupted layer of shiny ganoine, with the median ridge being more projected (Fig. 4A). Each ridge shows an accumulation of superposed ganoine strata (Fig. 4C). Under the ganoine is the dentine component (Fig. 4C) but with individualised concentrated units that sustain the ridges. These dentine units are organized around vascular canals (Fig. 4G) that may show loops (Fig. 4F); several dentine units are present under the well-developed ridges (Fig. 4C). In the groove that separates two ridges, the dentine units are thinner or missing. Under the dentine layer is a thick bony basal plate made of primary cellular bone with scarce vascular canals that are mostly restricted to the dentine units area (Fig. 4B, C). Reversely, the basal plate is crossed by numerous ascending canaliculi of Williamson (Fig. 4C, H), 2.5-5.5 μm in diameter; some of them cross the ganoine strata (Fig. 4D). Canaliculi of Williamson are frequently dichotomized (Fig. 4H). Obvious growth marks (Fig. 4C) indicate ecological seasonality. The ganoine layer shows rare traces of resorption of unknown ori-

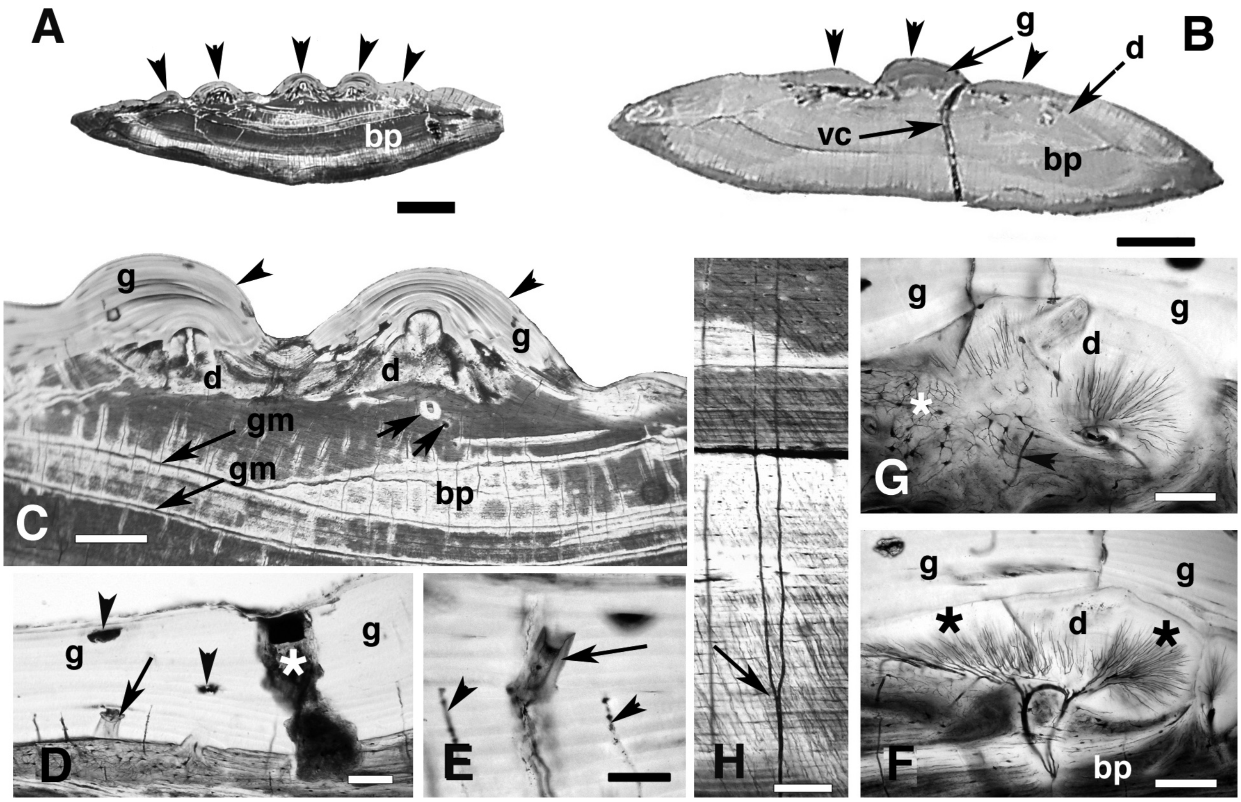

Figure 4. - Scales of *Obaichthys africanus* (MRS 45). **A-B**: Cross section of two scales (transmitted natural light), showing the three superimposed layers: pluristratified ganoine (**g**), dentine (**d**) and bony basal plate (**bp**); **A**: MNHN-Histos 1960. The arrowheads point to five ridges of ganoine. The basal plate (**bp**) is avascular; **B**: MNHN-Histos 1963. The arrowheads point to three ridges of ganoine. A vascular canal (**vc**) crosses the whole scale; **C-H**: Cross sections of scales (transmitted natural light); **C**: MNHN-Histos 1960. Detail of A showing the two median ridges (arrowheads) constituted of pluristratified ganoine (**g**), each one above a dentine unit (**d**). The two ridges lie on an avascular bony basal plate crossed by numerous canaliculi of Williamson. Two sections of vascular canals just below the right dentine unit are visible (arrows). Notice the growth marks (**gm**) in the basal plate (**bp**); **D**: MNHN-Histos 1964. Detail of the ganoine layer (**g**) showing two odontode bases (arrows) and a resorbed area (asterisk) characterized by its irregular alveolate walls. Two minor remodelling areas (arrowheads) are seen in the ganoine layer; **E**: MNHN-Histos 1964. Detail of an odontode base (arrow) in the ganoine layer. One can also show two canaliculi of Williamson crossing the ganoine strata (arrowheads); **F**: MNHN-Histos 1964. Detail of a dentine unit (**d**) organized above a vascular loop coming from the basal plate (**bp**), with numerous odontoblastic canalicles (black asterisks). (**g** = ganoine); **G**: MNHN-Histos 1964. Detail of a dentine bulk (**d**) subtending a ganoine ridge (**g**). The odontoblastic canalicles radiating from the vascular ramification are visible. A canaliculus of Williamson (arrowhead), and some osteocytes in the bony basal plate (white asterisk) are visible; **H**: MNHN-Histos 1963). Detail of the bony basal plate showing a dichotomized canaliculus of Williamson (arrow). Scale bars: A, B = 1 mm; C = 250 μm; D, F = 100 μm; E = 100 μm).

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Figure 5. - Scales of *Bawitius*. **A**: Cross section of a large scale (MNHN-Histos 1973) showing three patches of ganoine (**g**), the only two lateral ones being visible at the scale surface. Notice the growth marks in the basal plate (arrows) and the ascending vascular canals (arrowheads). **d**: dentine; **bp**: basal plate; **B**: Transverse section (MNHN-Histos 1967; natural transmitted light). Three superposed regions can be recognised from the surface to the deep: ganoine layer (arrowheads), dentine layer (**d**) and a bony basal plate (**bp**); the arrows point to wide vascular canals; **C**: MNHN-Histos 1967; polarized light. The plywood-like organisation (= elasmodine; white arrow) between the dentine layer (**d**) and the basal plate (**bp**) is visible. The basal plate is crossed by Sharpey's fibres (white asterisk). The square indicates the localization of H. **g**: ganoine; **D**: Cross section (MNHN-Histos 1983; natural transmitted light) of a small scale showing a ganoine ridge (**g**), bordered by the dentine layer (**d**) that shows numerous vascular canals (arrowheads); **E**: Cross section of a small scale (MNHN-Histos 1975). The upper half and the lower half of the section are respectively observed with polarized light and transmitted natural light. The regular organization of the lateral sides of the two stratified ganoine ridges show that patch organisation of ganoine does not result from a previous resorption. **d**: dentine; **g**: ganoine; **F**: Cross section of a small scale (MNHN-Histos 1979; natural transmitted light). Detail of the thick dentine layer. Numerous odontoblastic canaliculi (*), vascular canals (**vc**), primary denteones (**dtI**) and two secondary denteones (**dtII**) are visible; **G**: Detail of the inner part of dentine layer (MNHN-Histos 1972) that shows alternative opaque and lighted strata (black asterisk) above a secondary vascular cavity the bony wall of which is secondary bone (arrowheads); **H**: Cross section (MNHN-Histos 1967; natural transmitted light). Detail showing a secondary denteone (**OdII**) in the dentine layer (**d**), and two secondary osteones (black arrowheads) in the basal plate (**bp**) where we can also see Sharpey's fibres (white asterisks) and vascular canals (**vc**); **I**: Detail (MNHN-Histos 1973) of polarized osteocytes (arrows) on each side of a vascular canal (white asterisk). (scale bar = 50 μm). **J**: Detail (MNHN-Histos 1983) showing an ascending vascular canal (**vc**) that is surrounded by polarized osteocytes (black arrowheads). Scale bars: A, B = 1 mm; C, D = 250 μm; E = 200 μm; F-J = 50 μm).

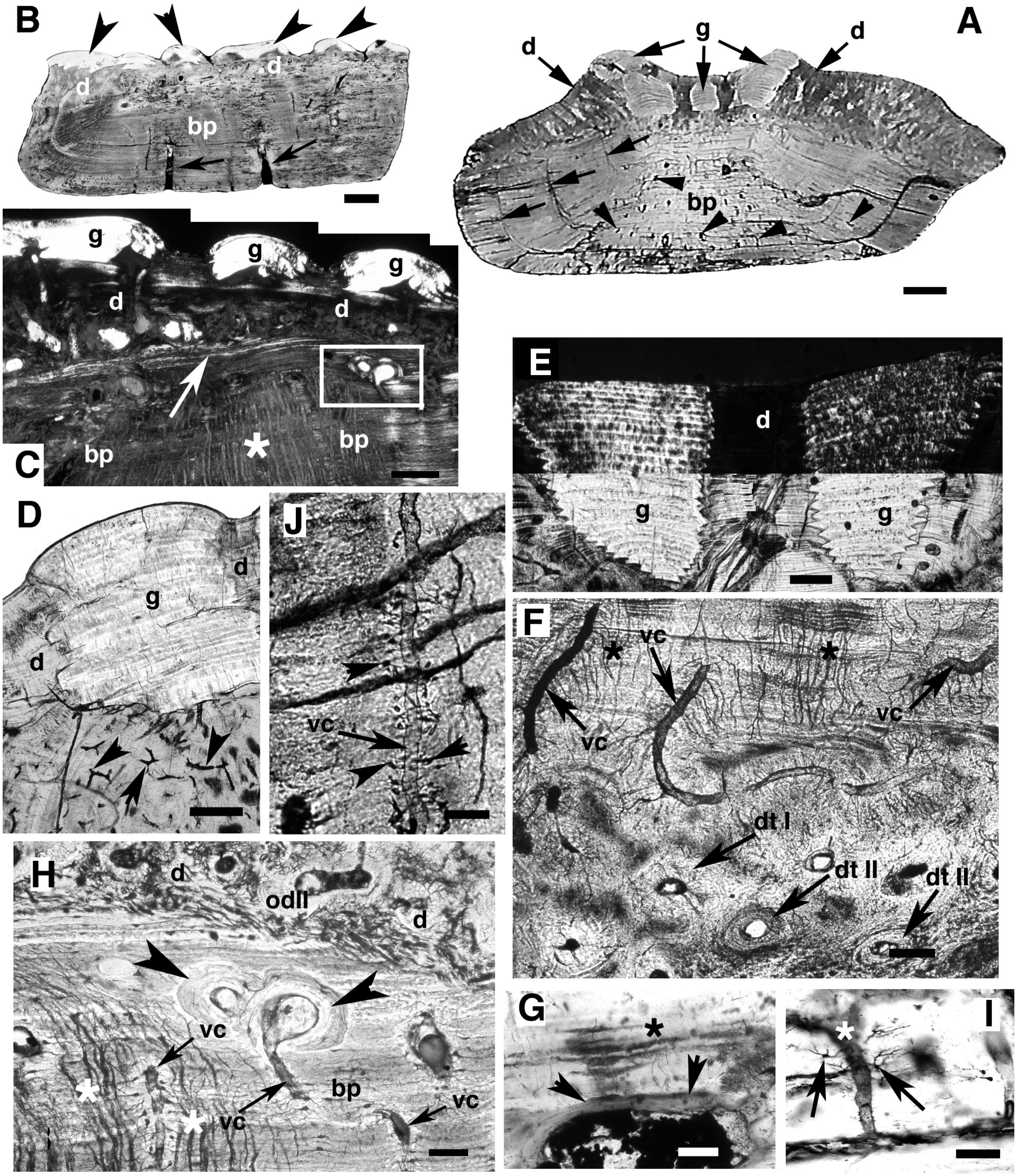

Figure 5. - Legends on opposite page.

gin, which are overlain by new ganoine deposits (Fig. 4D). Sometimes the erosive process affected the whole thickness of the ganoine layer and by places the underlying dentine (Fig. 4D). Odontodes are located within the ganoine. Their apex has been eroded before the deposit of new ganoine strata (Fig. 4D, E).

Types III and IV. Bawitius *(Fig. 5A-J)*

The large and small scales referred to the palaeoniscoid type are both formed of three main layers: 1) the surface of the scale bears either ramified ganoine rows or ganoine piles (Fig. 5A-C). In each case, ganoine is pluristratified and birefringent (Fig. 5B, C). The lateral sides of each strata end as a thin and sharp layer (Fig. 5E). As already noticed by Smith *et al*. (2006), the ganoine surface is perfectly smooth and deprived of microtubercles as described above. Such tubercles are generally present in polypterid and lepidosteoid scales (Gayet and Meunier, 1986; Meunier and Gayet, 1996; Daget *et al*., 2001). 2) A thick vascularized dentine layer (Fig. 5B-D) crossed by numerous odontoblastic canalicles (Fig. 5F) developing from the vascular canal walls constituting primary denteones (Figs 5F, H). Secondary denteones (Figs 5G, H) resulting from a remodelling process of dentinous tissue are also present. On the scale surface, dentine separates ganoine patches (Fig. 5A, C, E). In areas not overlain by ganoine, the odontoblastic canalicles of dentine start from the scale surface. Some vascular canals emerge at the scale surface. In the middle region of the dentine layer, regularly arranged strata are visible as alternating light and dark layers (Fig. 5C, G). 3) A thick basal plate made of cellular pseudo-lamellar bone (Figs 5A-C, H) and showing many ascending vascular canals (Figs 5A, B), some of which are connected to the vascular network of the dentine layer. These ascending canals of the basal plate are surrounded by polarized osteocytes lacunae (Fig. 5I, J). In the basal plate, there are also numerous Sharpey's fibres (Fig. 5C, H), which represent ligaments fastening the scale to their neighbouring ones and/or to the stratum compactum of the dermis. On some sections (not shown), obvious growth marks indicate ecological seasonality. Canaliculi of Williamson are lacking. Secondary vascular canals, the walls of which are constituted of secondary bone, are separated from the surrounding primary bone by cementing lines (Fig. 5F, H).

DISCUSSION

Adrianaichthys pankowskii

Lepidotes was used as a wastebasket and non-monophyletic genus gathering numerous species. The type-species is *L. gigas* from the Early Jurassic and the other species referred on sound systematic reasons are also early Jurassic in age (López-Arbarello, 2012). During the last years, some Late Jurassic species previously referred to *Lepidotes* have been attributed to other genera (i.e. López-Arbarello and Sferco, 2011). In the Early Cretaceous, most *Lepidotes* species were also referred to other genera and most of them are included in the Lepisosteiformes, a clade of ginglymodians containing the extant gars (Cavin, 2010; Cavin *et al*., 2013; Deesri *et al*., 2014). *Adrianaichthys pankowskii* constitutes a new occurrence of a lepisosteiform in the Cretaceous.

Obaichthys africanus

Dentine. – The organisation of the scales with three layers (ganoine, dentine, bony basal plate) is typical of the palaeoniscoid type as defined by Goodrich (1907). This author also defined the lepidosteoid type on the basis of absence of dentine, which is the situation present in all extant Lepisosteidae. Although *Obaichthys africanus* is clearly a lepisosteiform on the basis of osteological characters, the thick dentine layer in its scales does not fit with the definition of the lepidosteoid type, which is normally present in this group. Dentine has also been observed in the scales of South American extinct obaichthyids (Brito *et al*., 2000). Nevertheless, in *O. africanus,* the dentine units are more developed than in the scales of *O. decoratus* and *Dentilepisosteus laevis* (Brito *et al*., 2000). On the basis of this feature, *O. africanus* appears more primitive than *O. decoratus* and of *Dentilepisosteus laevis*, which are, however, less derived than the extant Lepisosteidae *Lepisosteus* and *Atractosteus*, which both possess typical lepidosteoid scales.

Odontodes in the ganoine layer. – The first descriptions of lepidosteoid scales already mentioned the presence of odontodes fixed on the external ganoine layer (Williamson, 1849; Nickerson, 1893). This observation was confirmed on the scales of *Lepisosteus oculatus* (Sire, 1994). In aspidorhynchid scales, odontodes are also present on the ganoine surface (Brito and Meunier, 2000) as well as in polypterid scales (Hertwig, 1879; Géraudie, 1988), although in the latter they are often temporary. Our study shows that the scales of *O. africanus* had odontodes at their ganoine surface. These superficial odontodes were partly resorbed before the deposit of a new stratum of ganoine that covers their base. Contrary to *O. africanus*, however, the scales of *O. decoratus* and *Dentilepisosteus laevis* do not show odontodes imbedded within the ganoine (Brito *et al*., 2000).

Bawitius

Weiler (1935) attributed to *Stromerichthys* isolated maxillae from Bahariya that Cavin *et al*. (2015) later referred to a polypterid, possibly *Bawitius* Grandstaff *et al*., 2012. A fragment of a maxilla similar in shape was also described from the Kem Kem beds in Morocco (Cavin *et al*., 2015). Schaal (1984) attributed an isolated ectopterygoid from Bahariya to *Polypterus? bartheli* and Grandstaff *et al*. (2012) later coined the genus *Bawitius* for this species. In Bahariya isolated scales similar to those described here were referred to a polypterid (Stromer, 1925, 1936; Schaal, 1984; Grandstaff *et al.*, 2012). In the Kem Kem beds, Dutheil (1999a) recorded the occurrence of polypterids represented by isolated pinnulae and he described a small species of polypterid, *Serenoichthys kemkemensis* Dutheil, 1999b from a clay lens called OT1 interpreted as a quiet lake or pool. Cavin *et al.* (2015) and Benyoucef *et al.* (2015) referred scales similar to those described here from the Kem Kem beds in Morocco and from coeaval beds in the Bechar basin in Algeria, respectively, to a polypterid, possibly *Bawitius*. Therefore, the scales described here are referred to *Bawitius* Grandstaff *et al.*, 2012.

Contrary to the opinion of Smith *et al.* (2006), we do not regard as secondary and resulting from a resorption of a primary continuous ganoine layer, the interrupted surface of ganoine in the scales referred here to *Bawitius*. This interrupted arrangement of ganoine is instead the standard and original state in this genus. This interpretation rests on the absence of resorption traces, which should have been present either in the lateral sides of the ganoine patches or in any stratum at the surface of a pile. On the contrary, the scales of *Callipurbeckia tendaguruensis*, for example, show typical resorption lacunae (= Howship's lacunae) on their ganoine surface (Arratia and Schultze, 1999, fig. 12). Moreover the dentine that fringes the ganoine is also deprived of resorption traces that normally appear as discontinuities in the structure (compare our Fig. 3E to the scales of *Lepidotyle* in Meunier and Gayet, 1992, figs 9-12). Moreover, no scales showing a regular continuous surface of ganoine associated with the characteristic histological organisation of a "palaeonisciform" fish have been found in the Kem Kem beds, an observation that reinforces our hypothesis of an initial discontinuity rather than a resorption of the ganoine.

In the two palaeoniscoid-types of scales, we observed the presence of a plywood-like organisation of collagen fibres. The regular arrangement of these strata, located between the dentine layer and the bony basal plate, has been recorded in the scales of extant Polypteriformes (see Sire 1989, 1990), as well as in fossil ones (Gayet and Meunier, 1991; Meunier and Gayet, 1996; Daget *et al.*, 2001). This observation is strengthened by the presence of polarized osteocytes that surround the ascending vascular canals as described in a number of Polypteriformes. This peculiar organisation has been first noticed in several fossil Palaeonisciformes (Schultze, 1968; Ørvig, 1978), in extant polypterids (Ørvig, 1957; Sire, 1989, 1990) and then in fossil Polypteriformes (Meunier and Gayet, 1996). Our isolated scales from the Tabaste's collection and from new collection from the Kem Kem beds resemble various other scale material described in the literature, such as the Cenomanian of Bahariya, Egypt (Stromer, 1925, 1936; Smith *et al.*, 2006), and the lower Cretaceous of Ubangui formation (Congo) (Casier, 1961: Pl IV, figs 10, 11).

The studied thick rhomboid "patches" and "ridged" scales from upper Cretaceous Moroccan Sahara, with the three superimposed layers – ganoine, dentine and bony basal plate – are 'true' ganoid scales (Goodrich, 1907; Kerr, 1952; Schultze, 1977; Meunier, 1980; Sire *et al.*, 2009). But the important reduction of the superficial shiny ganoine, forming either parallel ridges, with or without ramifications, or thick irregular patches, gives them an original status among the ganoid scales. The bony basal plate of the two series of scales is totally devoid of canaliculi of Williamson. Consequently, this fossil material cannot be allocated to a holostean fish, which are characterized by the occurrence of such canalicles (Nickerson, 1893; Goodrich, 1913; Ørvig, 1951; Moss, 1964; Schultze, 1966; Francillon-Vieillot *et al.*, 1990; Sire and Meunier, 1994; Meunier, 2011). Accordingly, the attribution of these scales by Tabaste (1963) and Weiler (1935) to semionotids is wrong. In return, the three described layers in types III and IV fit well with a paleoniscoid scale type (Goodrich, 1907; Schultze, 1968, 1977, 1996; Meunier, 1980; Meunier and Brito, 2004; Sire *et al.*, 2009). These scales, moreover, share characters with the polypteriforms: *i*) in the basal plate, there are ascending vascular canals surrounded by osteocytes closed to the osteocytic canalicles, which are polarized. Such an organisation has already been described in the scales of the paleoniscid *Scanilepis* (Ørvig, 1978) and in the polypteriform *Latinopollia* (Meunier and Gayet, 1996, 1998); it is also known in extant Polypteridae (Meunier and Gayet, 1996; Daget *et al.*, 2001); *ii*) there is an elasmodine layer (Schultze, 1996; Sire *et al.*, 2009), a plywood-like organisation of collagenous fibres between the dentine layer and the oldest part of the bony basal plate (Fig. 5C, G). Such a structure has been first described in the scales of the extant polypterid *Polypterus senegalus* (Sire, 1989, 1990). Later this typical elasmodine layer has been also observed in various fossil Polypteridae from the Cretaceous of Africa (Gayet *et al.*, 1988; Daget *et al.*, 2001; Smith *et al.*, 2006), in *Dagetella sudamericana* (Gayet and Meunier, 1992) and *Latinopollia suarezi* (Meunier and Gayet, 1996) from the Cretaceous of Bolivia, and in *Bartschichthys* sp. from Maranhão state of Brazil (Dutra and Malabarba, 2001). The elasmodine is regarded as an autapomorphy of the Polypteriformes. Consequently, the presence of a plywood-like organisation between the dentine layer and the bony basal plate provides further evidence to include *Bawitius* into Polypteriformes (Daget *et al.*, 2001).

The absence of morphological and histological differences between the structure of large and small scales of types III and IV indicates that both kinds likely belong to the same taxon, possibly *Bawitius*. Presence of an interrupted ganoine layer in the small scales, i.e. from young individuals, is further evidence that the ganoine is not resorbed during ontogeny.

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